along the ventral wall of the rectum; at the second curve, which forms a sharp kink, two muscular bands or retractors are attached, the other ends of which run to the ventral wall of the rectum. On each side of the rectum are situated four glandular masses of spherical shape. Three of these (α, β, and γ) are shown in the diagram (fig. 10); the fourth one is small and is hidden by the one marked γ. On section γ shows a series of concentric fibrous planes of a pale colour, while the darker soft tissue between is on microscopic examination seen to be glandular. Prof. A. H. Young has referred in detail to these bodies in the Koala (Journ. Anat. & Phys. vol. xiii. p. 316), and he has pointed out that, while three of them are Cowperian glands, the fourth (corresponding to α in fig. 10) is one half of the divided corpus spongiosum. This conclusion a section of α compared with that of γ seemed to bear out, though the specimen had not been well enough preserved for careful microscopic study.

Further Notes on the Lemurs, with especial Reference to the Brain. By G. Elliot Smith, M.D. (Communicated by Prof. G. B. Howes, D.Sc., LL.D., F.R.S., Sec.L.S.)

[Read 5th March, 1903.]

(With 4 text-figures.)

Since my memoir on the Prosimian brain was presented to the Society *, I have come into possession of some valuable material which is of sufficient interest to call for these additional notes. At the same time, I shall avail myself of the opportunity of referring to some interesting communications of Hubrecht † and Earle ‡, with which I was not acquainted when my memoir was written. Professor Howes has called my attention to these, and generously lent me copies of them.

* Trans. Linn. Soc., Ser. II. Zool. vol. viii. pp. 319–432. References in this paper under "Mem." refer to the illustrations of the memoir.

† A. A. W. Hubrecht, "The Descent of the Primates," Princeton Lectures, New York, 1897. (Compare also "Die Keimblase von Tarsius," Festschrift für Carl Gegenbaur, Leipsig, 1896.)

‡ Charles Earle, "The Lemurs as Ancestors of the Apes," 'Natural Science,' vol. x. no. 63, May 1897.

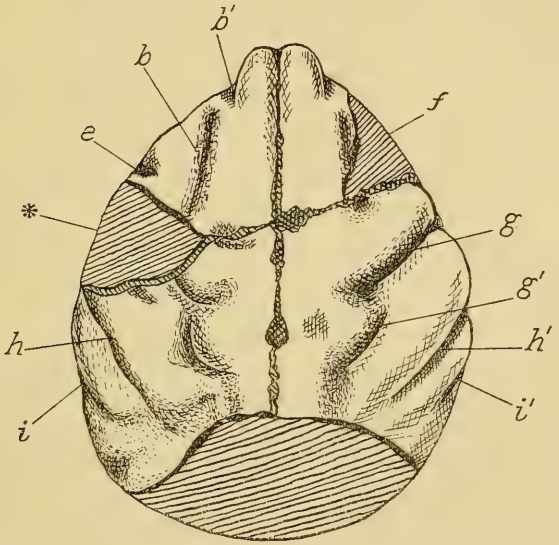
Id., "On the Affinities of *Tarsius*: a Contribution to the Phylogeny of the Primates," The American Naturalist, vol. xxxi. July 1897, pp. 367 *et seq.*

The Brain of Globilemur.

The consideration of the features of this brain led me in my Memoir to such indecisive and unsatisfactory results, that no apology is needed for again returning to the study of a form of such interest.

The British Museum has recently acquired fragments of two crania of *Nesopithecus*, a genus which is either identical with or very closely related to *Globilemur*. Plaster moulds of the brain-cavity of these fragments were made, and, at the kind suggestion of Dr. Forsyth Major, replicas of the casts were sent to me by Dr. Smith Woodward.

Fig. A.



One of these (fig. A) represents a considerable part of the dorsal aspect of the brain; but, unfortunately, it does not show any part below the level of the reference-line *g* in fig. 40 of my memoir. The second cast represents only the anterior extremities of the cerebral hemispheres, *i. e.* the area containing the coronal, diagonal, and orbital sulci.

Unlike the complete cast described in the body of my memoir (Mem. figs. 39 and 40), these two fragments exhibit deep and exceedingly well-defined sulci. This fact, however, only renders the incompleteness of the specimens all the more tantalizing,

since the information which would be conveyed by the small missing fragments (fig. A, * and *f*) would have enabled us to decide with absolute certainty all the doubtful issues raised in the previous discussion.

In the smaller fragment, the coronal and diagonal sulci are exceptionally deep and sharply defined, so that their identity is placed beyond all doubt. In shape and position they closely resemble the furrows *b* and *e* (Mem. fig. 40) in the type-specimen. In the other specimen (fig. A) the coronal sulcus is broken up on both sides into a small anterior (? prorean) fragment (*b'*) and a long posterior sagittal furrow (*b*). The gyrus included between the coronal sulcus and the interhemispheral cleft is 7 mm. broad in front and 11 mm. broad at its posterior extremity. The relative smallness of this gyrus is in marked contrast with its size in the Apes and even in most Lemurs. Thus the corresponding measurements in a specimen of *Cercopithecus patas* are 6 mm. and 20 mm. respectively, and in a *Lemur macaco* 4 mm. and 13 mm. respectively. In other words, both in Apes and Lemurs the coronal sulcus is more oblique and the area to its mesial side more extensive than in *Nesopithecus*. In this particular *Nesopithecus* approximates nearer to the primitive condition than either *Lemur* or *Cercopithecus*.

The position of the diagonal sulcus (*e*) is noteworthy. In the Indrisinæ this furrow is placed within the orbital depression, *i. e.* below the orbital margin; in *Lemur* it extends on to the orbital margin, but is placed mainly in the orbital depression; whereas in *Nesopithecus* (*Globilemur*) it is placed *wholly above* the orbital margin. In this respect *Globilemur* resembles the Apes.

The long furrow labelled *g* in the type-specimen (Mem. figs. 39 and 40) is in the present one seen to consist of two separate sulci—an obliquely-placed anterior element (*g*), the upper extremity of which overlaps a small comma-shaped furrow (*g'*). The latter almost certainly represents a "lateral" (intraparietal) sulcus. I cannot confidently express a definite opinion as to the identity of the furrow labelled *g*, *i. e.* the anterior oblique element; but the condition exhibited in this specimen does not lend any support to the view that it is in any part of the Sylvian fissure. Nor can I confidently regard it as a separate part of the lateral, because such a breaking-up of that is almost unknown, except in the Simiidæ and Man.

A direct comparison of this brain with that of an Ape, and especially such an Ape as *Cebus*, suggests the identity of this furrow (*g*) with the sulcus centralis (Rolandi).

If this is so—and the imperfect state of the specimen does not permit me to do more than suggest the interpretation—the position and direction of the sulcus are distinctly pithecoid, and in marked contrast with the Prosimian relations of the central sulcus.

Perhaps the most interesting feature in this cast is the existence of a well-defined furrow, corresponding to the slight depression labelled *h* (which I represented in a very doubtful manner in figs. 39 and 40 of my memoir). The fragment containing the lower end of this sulcus is unfortunatety missing. Nevertheless it seems probable that this furrow represents the Sylvian fissure, having a position and an extremely oblique direction such as are found elsewhere only in the Apes. Behind it there is a second oblique furrow (*i*), which must be the parallel (postsylvian) sulcus, if *h* be regarded as the Sylvian fissure.

The shape of the brain and the disposition of its furrows in *Nesopithecus* are therefore much more pithecoid than those of any other Prosimian, and, in Forsyth Major's words, it "departs from the Lemurids and approaches the Cebidæ and Cercopithecidæ" (Proc. Royal Society, vol. lxii. 1898). In spite of these resemblances to the Apes, the conformation of the olfactory region of the brain and the relations of cerebrum to cerebellum point decisively to the Prosimian status of *Globilemur*.

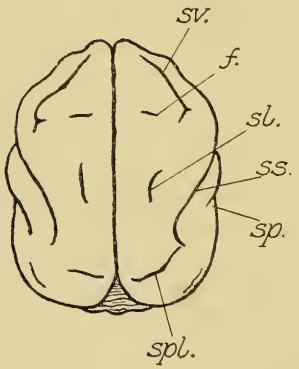
If this interpretation of the sulci is correct (and, with the knowledge of the condition presented by this specimen, I cannot suggest any alternative scheme which is even plausible), the brain of *Nesopithecus* presents a strange mixture of decidedly pithecoid and equally decided Prosimian features side by side. The shape of the brain is distinctly Cercopithecoid, the plan and direction of its sulci (and consequently the mode of subdivision of the neopallium) diverge widely from the common Lemurid arrangement, and closely resemble those of the Cebidæ and Cercopithecidæ. On the other hand, there are the distinctly Prosimian characters already mentioned, and yet *Nesopithecus*, unlike the other connecting link, *Tarsius*, shows no indications of being a primitive type. To attempt to explain this strangely mixed association of characters on the evidence of the brain would be sheer guesswork. In fact one could wish for no

stronger argument to oppose to those who hold that Lemurs and Apes belong to separate orders, than the mere exhibition of the brain of *Nesopithecus*.

The Brain of Propithecus.

When the memoir on the Prosimian brain was written I had not seen the actual brain of any of the Indrisinæ, and had to draw my data from the examination of cranial casts, studied, however, in the light of Milne-Edwards's descriptions of the actual brains. Within the last three months Professor J. T. Wilson, of the University of Sydney, has kindly placed at my disposal a series of young and fœtal Indrisinæ labelled "*Indris diadema*," which had been in spirit for a considerable time in the stores

Fig. B.



of the Australian Museum. In the oldest specimen (in which the first teeth were just cutting the gums) the full complement of cerebral sulci was present; but in the rest no furrows, except the hippocampal and rhinal fissures, had yet made their appearance.

I shall merely describe the arrangement of the sulci and the most salient features of the largest specimen. The length of the cerebral hemisphere is 31 mm., and the breadth of the two hemispheres 26·5 mm. As Milne-Edwards and Forsyth Major have already observed in reference to the young *Propithecus*, the cerebellum is almost completely hidden by the cerebrum (fig B). That this covering of the cerebellum is really due to an exceptionally great caudal extension of the cerebrum is shown by

an examination of the mesial aspect of the hemisphere (fig. C). In this specimen 12 mm. out of a total length of 31 mm. lie on the caudal side of the splenium of the corpus callosum; whereas in an adult *Lemur fulvus* only 11 mm. out of a total length of 41 mm. lie behind the splenium.

There is a typical coronal sulcus (*s.co.*) with a bifid posterior extremity such as commonly occurs in the genus *Lemur* (Mem. fig. 1), *Globilemur* (Mem. figs. 39 & 40), and, perhaps, in *Indris* (Mem. fig. 30). This exact form of coronal sulcus was present in only one (Mem. fig. 29) of the crania of *Propithecus* examined.

Both the orbital and diagonal sulci present a simple linear form, and occupy that peculiar position entirely within the

Fig. C.

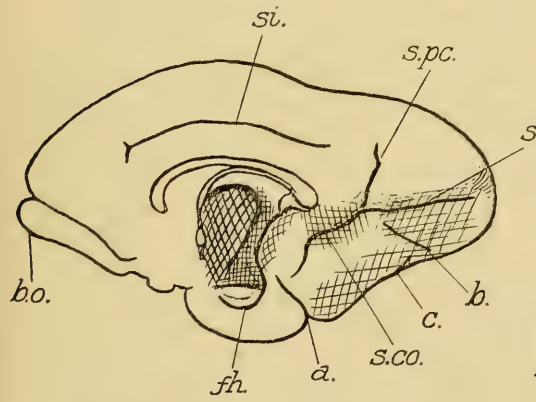
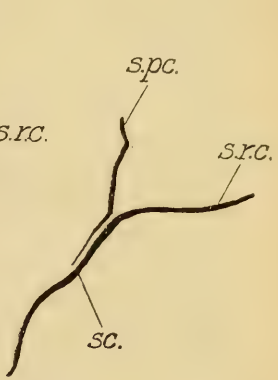


Fig. C'.



orbital area which seems to be so characteristic of the Indrisinæ (Mem. fig. 28). The orbital sulcus is placed very close to and parallel with the olfactory bulb, whereas the diagonal sulcus is parallel to and entirely below the orbital margin.

As we have already noticed in some of the casts of *Propithecus* (Mem. fig. 22), the sulcus *f* (*i. e.* the supposed dorsal element of the central sulcus) is distinctly transverse, and not oblique as in *Lemur* and *Nycticebus*.

This specimen resembles *Indris* and differs from all my specimens of *Propithecus* (with the possible exception of that represented in Mem. fig. 29) in regard to the form of the Sylvian fissure and the lateral sulcus. The latter (fig. B, *sl.*) is exceedingly

small, and is far removed both from the coronal (*sco.*) and post-lateral (*spl.*) sulci. To compensate for its diminutive size, the suprasylvian sulcus (*ss.*) is prolonged far back into a hook-like extremity; and on the right hemisphere it almost fuses with the lateral extremity of the post-lateral sulcus (*spl.*). It is instructive to recall in this connection that in those Apes, such as the Lemurine Dourocoli (*Aotus felinus*), in which the sulcus intra-parietalis becomes confluent with the suprasylvian sulcus, a small furrow persists in the position where the anterior end of the intraparietal (lateral) sulcus would be found if the fusion had not taken place (*vide* fig. 229, p. 391, Catalogue of the Royal College of Surgeons, 2nd edition, vol. ii.). This seems to point to the conclusion that in those Lemurs (e. g. *Nycticebus*) and Apes (many of the Cebidæ) in which the suprasylvian (Sylvian) and lateral (intraparietal) sulci appear to become confluent, it is a case of the more stable suprasylvian sulcus being mechanically prolonged, to relieve the tension of the expanding cortex, which would otherwise be accommodated by the lateral sulcus rather than a real confluence of the two sulci. In favour of this interpretation it is to be noted that a submerged gyrus indicating the site of the supposed union of the lateral and suprasylvian elements never occurs (so far as I am aware), whereas in those cases where two sulci become confluent (*e. g.* in the case of the calcarine-retrocalcarine junction) a submerged gyrus frequently occurs to indicate the site of the junction. On this hypothesis alone, it seems to me, can we explain the development in such cases of the aborted lateral element (fig. B, *sl.*).

Although the lower extremity of the suprasylvian sulcus does not emerge from the Sylvian complex on the surface of the brain (compare *Lemur*, *Perodicticus*, inter alia), the separation of the lips of the "Sylvian fissure" reveals the fact that it is composed of two distinct sulci (suprasylvian and pseudosylvian) bounding a triangular submerged area, as in the genus *Lemur* (Mem. fig. 6, *a*). It is of interest to note, however, that the opercular anterior lip of the suprasylvian sulcus is relatively greater (*i. e.* more pithecoid) than it is in the adult *Lemur*.

I can find no trace of the rhinal fissure, except on the mesial surface of the hemisphere (fig. C, *a*), where it presents a form such as we are already familiar with in *Lemur* (Mem. fig. 5, *a*).

There is a typical postsylvian sulcus (Mem. fig. 6, *sp.*).

On the mesial surface there is no rostral nor genual sulcus.

There is a typical long intercalary furrow (*si.*) and the characteristic triradiate calcarine group. The calcarine sulcus (*sc.*) is confluent with the retrocalcarine (*s.r.c.*). The paracalcarine sulcus (*s.pc.*) is separated from the calcarine by a deeply submerged narrow gyrus (fig. C').

The mesencephalic depression on the hemisphere is more extensive than it is in the adult *Lemur*, so that the calcarine sulcus is placed within it as far back as its apparent bifurcation.

The furrows *b* and *c*, already noted in the brain of *Lemur* (Mem. fig. 5), are present here also.

There is a small hippocampal tubercle. There is no posterior cornu of the lateral ventricle.

The cerebellum so closely resembles that of *Lemur* that no special account is demanded.

The extraordinary variability of the disposition of the sulci in *Propithecus* is such as could have been produced only by retrogressive changes from a type more richly supplied with cerebral furrows.

The Brain of Lemur macaco.

I trust to have abundantly shown in the body of the aforenamed memoir that the great desideratum in the study of an organ which exhibits great variability is a large number of accurate records. No apology is needed, therefore, for adding notes, even in reference to the genus *Lemur*.

I have recently received from Captain Stanley Flower the body of an adult female *Lemur macaco*, from which I obtained a fresh brain.

The cerebellum is exposed to the same extent as that delineated in fig. 3 of my memoir. The cerebral hemisphere is 46 mm. long, and the two hemispheres together 37 mm. broad.

The rhinal fissure presents the usual form (*cf.* Mem. fig. 7), only the angle being definitely developed.

The orbital and diagonal sulci are present and well-developed, and occupy the positions characteristic of the genus *Lemur* (Mem. fig. 6), *i. e.* the diagonal does not cross the orbital margin.

There is an extensive, simple, linear coronal sulcus on the right hemisphere; on the left side its caudal end is bifid; a simple, obliquely-placed, comma-shaped sulcus *f* in the usual position (Mem. fig. 1); the extensive lateral sulci are symmetrical, and both resemble that shown on the left hemisphere

in the figure. The upper end of the suprasylvian sulcus is also disposed like that of the left hemisphere in Mem. fig. 1; the upper end of the postsylvian sulcus is bent forward, very slightly on the right hemisphere, but more decidedly on the left side (compare Mem. fig. 7). The lower end of the suprasylvian sulcus is exposed on the surface to an exceptionally great extent.

Fig. 4 of the memoir accurately represents the basal surface of this specimen in all except three points: the rhinal fissure (*fr.*) is incomplete, the diagonal sulci (*sd.*) do not extend to the margins of the orbital surfaces, and the lower end of the suprasylvian sulcus (*i. e.* its exposed part) is distinctly visible.

The mesial surface of each hemisphere is exactly like that represented in fig. 5 of the memoir in every respect, except that there is no genual sulcus (*sg.*) and the intercalary sulcus is shorter, *i. e.* does not extend backward so far.

General Considerations.

In the memoir on the Prosimian brain I disclaimed any pretension to settle the question as to the relationship of the Lemurs to the Apes and other Mammalia, and merely attempted to state in decided and unequivocal language the nature and value of the evidence of cerebral anatomy concerning the vexed question of kinship. No problem as to the closeness of the bonds of affinity which link together various mammalian families can be adequately decided on the evidence of one region of the body alone, even though this be so important and representative an organ as the brain.

I return to this aspect of the subject only because I was ignorant of the above quoted memoirs of Hubrecht and Earle when my memoir was written.

The aim of Hubrecht's researches is chiefly to demonstrate the intimate relationship of *Tarsius* to the Apes, and the wide gap which separates it from the Lemurs. In his own words:—"*Tarsius* is not a Lemur at all, . . . it should never have been placed alongside the Lemurs, . . . its position is somewhere between an unknown type of Insectivores and our modern monkeys and Man" (*op. cit.* p. 16).

These views are based chiefly on the evidence of placental anatomy, the validity of which Sir William Turner long ago refused to acknowledge, in view of the fact that the testimony of the teeth, the skeleton, the unguiculate digits, the calcarine

region of the brain, and the mammary glands points to a different conclusion. Hubrecht calls in the evidence of the teeth to support his contention; but, as Leche and Earle (*op. cit.*) have demonstrated, the full study of the teeth of *Tarsius* shows it to be "a Lemur beyond all doubt." The arguments of Hubrecht have been so thoroughly criticized by Earle in the memoirs quoted, that it is quite unnecessary to enter into details here. In opposition to Hubrecht's statements that in "very many respects *Tarsius* does not fit in with the Lemurs at all," and that its incisors and canines "resemble more closely those of the Insectivora than [those] . . . of the Lemurs" (*op. cit.* p. 11), it is, however, well to recall the fact that the brain of *Tarsius* exhibits decisive evidence of its Lemuroid status in the calcarine region, in the Sylvian fissure, and in numerous other traits which have been enumerated in the body of my memoir. In the degree of caudal extension of its hemispheres, it is even farther removed from the Insectivora and more pithecoid than the Lemurs.

Hubrecht's memoir is of special interest, because it emphasizes the undoubted fact that *Tarsius* is more nearly related to the Apes than are the Lemurs. This is also demonstrated in the brain by the relative microsmatism, the great caudal extension of the hemispheres, and the presence of a definite posterior cornu in the lateral ventricle. But the evidence of cerebral anatomy lends no more support than, I believe, the structure of the rest of the body does to the view that the approximation of *Tarsius* to the Apes implies its separation from the Lemurs. So far as its brain is concerned, *Tarsius* is a "Lemur of Lemurs," to use an expression of Professor Howes: it is certainly more nearly related to the Apes than most other Lemurs; but, on the other hand, all the Apes and Lemurs are linked by a much closer bond of affinity the one to the other than are any of them to the other mammals. *Tarsius* is unquestionably the most primitive living Primate.

I have not deemed it necessary to refer in detail to the excellent memoirs of Charles Earle, because they so nearly express the views to which I have been led from the study of the brain.